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XIII.—Observations on the Genera Pachybdella (Diesing) and Peltogaster (Rathke), two animal forms parasitic upon the abdomen of Crabs. By Professor STEENSTRUP*.

In the most recent systematic work on the Worms, Intestinal Worms and the lower division of the great Articulated series in general, Diesing's 'Systema Helminthum' (1850, vol. i. p. 434-435), we find amongst the Bdellidea, in the suborder Monocotylea, subtribe Cephalobdellida, a new genus Pachybdella, established upon a parasitic animal discovered some years before by Rathke under the abdomen of the common Crab, Carcinus Manas, and described by him under the name of Peltogaster Carcini+. Diesing himself appears to have had no specimens of the animal before him, but to have merely drawn up his generic and specific characters from Rathke's descriptions and figures. which again are founded upon two specimens of this remarkable parasite, one of which was obtained from the Norwegian coast, the other from the Black Sea. Neither Rathke's description nor his figures, however, furnish a sufficient notion of the structure of the animal to enable us to arrive at any definite conclusion as to its systematic position, or as to the group, whose characteristic marks it might have lost in consequence of its parasitic existence. It is only from the circumstance that Rathke refers the animal to the genus Peltogaster, which had been recently established by him, and of which he has more fully described another species ± (P. Paquri, Rathke), from the abdomen of the Hermit Crab, that we learn that this author would

* From Wiegmann's Archiv. 1855, No. 1. p. 15.

* Nova Acta Acad. Cæs. Leop. Car. 1843, tom. xx. pt. 1. pp. 244–249.
* Partly in the same paper, p. 245–247, and partly in the Neuest. Schr.

der Nat. Ges. in Danzig, 1842, Bd. ii. p. 105-111.

Ann. & Mag. N. Hist. Ser. 2. Vol. xvi.

11

place the genus *Pachybdella* amongst the Vermes, accepting this class in its widest sense. In this class, however, Rathke has given his genus no determinate place; he only thinks that these animals are by no means to be arranged with the Bdellide or Trematode worms, of which we are at once reminded by the form of their bodies, the pits with which they attach themselves, and their parasitic mode of life; he would rather regard them as transition forms from the Worms to the Actiniæ and the Radiated animals most nearly allied to these. Thus, according to his view, the pit with which these sac-like parasites attach themselves to the abdomen of the crab, is only a sucker, from which no tube leads into the body of the animal; and the other opening, which exists at the free extremity of the body, is a mouth, which leads into a large cavity, serving at once as a digestive cavity and for the development of the ova,-a double office which he considers to be proved by the extended observations which he was enabled to make upon the P. Paguri, but which we must admit with the author is "something very peculiar and hitherto unheard of in the case of a worm."

Our knowledge of Diesing's so-called genus *Pachybdella* is however fortunately not confined to the scanty information, welcome as it may be in every respect, which Rathke has furnished upon the individuals found and examined by him; other statements are extant, which, although they have hitherto been overlooked, are deserving of every attention, as they throw a light upon the distribution and systematic position of this parasite.

With regard to the occurrence and diffusion of *Pachybdella*, I will refer to the sac-like parasite found by Bell under the abdomen of *Carcinus Mænas* and *Portunus marmoreus* from the British Channel, and which he has described in such a manner, that there can be no doubt he had a *Pachybdella* before him. On the first-mentioned crab he appears to have found the parasite only occasionally, but it occurred in considerable numbers on the other. This author, who only refers to the parasite *en passant*, regards the pit by which it attaches itself as the oral aperture, and the other orifice, which Rathke considers to be the mouth, as the anus. Bell consequently ascribes a complete digestive canal to the animal. The parasites which occurred upon *Carcinus Mænas* were so similar to those which Bell found in greater abundance upon *Portunus marmoreus*, that he does not appear to have felt any doubt as to the identity of the species.

I can prove the occurrence of *Pachybdella* not only in the Channel, but also in the Mediterranean, from several individuals in the Zoological Museum of this University (Copenhagen). In the year 1848 I received a few Crustacea from the former locality,

from M. V. Prosch, a ship-surgeon, and amongst these was a *Portunus hirtellus*, under the abdomen of which there was a very large sac, which I took to be a Lernæid parasite, without however being able to refer it to any known form of the family of Lernæidæ. I have since, however, recognized in it a form approaching so closely to *Pachybdella Carcini*, that it could only be distinguished therefrom by a few immaterial points in the outline of the body, and the wrinkling of the hinder opening. From a specimen of *Carcinus Mænas*, taken by Captain Svenson on the "Black banks" in the North Sea, I obtained a very large individual of a form exactly agreeing with *P. Carcini*, Rathke; and I have since found three other individuals, resembling the first, in a bottle containing several specimens of *Portunus hirtellus* from the Mediterranean.

If the preceding statements would lead to the supposition that this form of parasite is by no means to be reckoned amongst the greatest rarities of these seas, this appears still more distinctly from some observations which I found in Cavolini's memoir upon the Development of Fishes and Crustacea, on reading it through last autumn with a very different object. From this I found that Cavolini had not only known and figured these animals, but that he had had them in quantity, and, as it appears from his figures, several species of them, found under the abdomen of two species of crabs, which are called Cancer depressus, Fabr., and C. verrucosus, Forsk., in his memoir. These sacs are found both upon the males and females; they are represented under the abdomen of the males of both species (tab. 2. figs. 1 & 14), and under that of the female of the former (fig. 13). They occur so commonly, that the fishermen are generally of opinion that the eggs of the crabs are contained in them. The form represented under the tail of the C. verrucosus in Cavolini's fig. 14, so closely resembles the P. Carcini figured by Rathke, that it might be taken for the same species; that represented in figs. 1 & 13 on *Cancer depressus* rather resembles the one above mentioned from Pagurus hirtellus, but Cavolini states that the opening at the narrow end has only four knots or teeth, whilst my specimens had at least twice that number (8-10). The comparison of the outline of the animal with that of the fruit of Thlaspi Bursa-pastoris is very characteristic, but shows that his specimens must have been somewhat longer in proportion than those which I obtained from *Pagurus hirtellus*.

From the above observations it is sufficiently evident, that these *Pachybdella*-like parasites are not only more abundant than has been supposed, but that several species of them occur, according to the various species of crabs upon which they live. But still more important consequences result from Cavolini's

investigations. He has traced the development of the eggs which fill these sacs in such enormous quantities, and ascertained that the young proceeding from the sacs from both species of crabs are of the same kind, and that the young is a true Crustaceous animal. He finds a resemblance between these young animals and the Cancer paludosus of Müller (Zool. Danica, tab. 48), but at the same thinks that they must be approximated to the Monoculus Telemus of Linnæus*. On tab. 2. fig. 15, Cavolini figures a portion of the eggs taken from "the sac" that is the Pachybdella, under the abdomen of the crab which he calls Cancer verrucosus; they are still immature, and are united by mucous threads into chains. Fig. 16 a. represents the mature egg with the developed embryo within it, and fig. 16 c, the embryo just after its exclusion from the egg, with three distinct pairs of swimming feet, provided with bristles. It cannot be denied that this embryo is exceedingly like that of many Entomostraca, and we might therefore be induced at first to regard the Pachybdella as a kind of Lernzeid animal. But as I must leave it to future observers, who may have the opportunity of collecting these animals in large quantities, to give a conclusive answer to this question, and only propose in the following pages to indicate some remarkable relations between the Pachybdellæ and other forms of Crustacea, I will only add here, that Cavolini, notwithstanding the experiments which he made with this view, did not succeed in tracing the further changes of this embryo, and that he, in accordance with the spirit of his time, did not suppose that the young animal itself might become converted into the sac in which the eggs were found, but rather that it was developed into a Crustacean, which afterwards fastened this ovisac under the abdomen of the crabs.

From Cavolini's observations, however, it appears that *Pachy-bdella* is undoubtedly a Crustacean, and one which is gradually brought into its sac-like form in consequence of its parasitic mode of life.

Even if we admit Diesing's separation of the original contents of Rathke's genus *Peltogaster*,—according to which the shorter and broader form with the sucking pit at one end of the body, which occurs under the abdomen of crabs, will form a peculiar genus under the name of *Pachybdella*, and this we may be so much the more inclined to do, as it appears from the preceding statements that there are several species exceedingly closely allied to it in external appearance,—we should certainly establish no

* The Monoculus Telemus, Linn., which Linnæus himself says is "generis etiamnum dubii," is very clearly from his diagnosis and description the Hyalæa tridentata of Forskäl.

more than a generic or subgeneric division, as the other half of the original contents of the genus appears to be so closely allied to this, and only to differ in the more elongated form of the body, in the position of the sucking pit further from the extremity, and almost under the middle of the body, and in the residence of the animal under the abdomen of a species belonging to another family of Crustacea (*Pagurus Bernhardus*). If therefore *Pachybdella* has proved to be a true Crustacean, analogy leads us to regard *Peltogaster* in the same light.

However, we need not perhaps rest entirely upon this conclusion, as there are certainly direct observations in existence that the young of the *Peltogaster*-like sacs found under the abdomen of the Macroura and Anomura (?) are Crustacean in form. Thus, Diesing has not noticed that Kröyer, in his Monograph of the Northern species of Hippolyte, has briefly mentioned the parasites by which they are infested, and especially certain sac-like creatures, which must undoubtedly be referred to the animals now under consideration*. In the fourth section of the Monograph, which bears the title of "Ein Paar Bemerkungen über Schmarotzerthiere auf Hippolyten," the author, after describing some other parasites, continues as follows (p. 56) :-- " Lastly, under the abdomen of Hippolyte pusiola, I discovered an enigmatical parasite (tab. 5. fig. 110 α) which it is difficult to refer to its right position,-nay, its structure appears so simple, so completely destitute of all organs, that one might perhaps easily be led to regard it, not as an independent animal, but as a mere pathological phænomenon, a swelling or excrescence on the Hippolyte[†]. It evidently forms a new genus, which on the one hand appears to have some analogy with the Lernæidæ, and on the other possesses an external affinity to some Hirudineæ and intestinal worms. Of this form I know several species : I found one of a whitish colour and of considerable size, in abundance on the abdomen of Pagurus pubescens near Spitzbergen; another, smaller and of an orange-red colour, occurred on Pagurus Bernhardus in the Kattegatt ; the third, which occurs on Hippolyte pusiola, is nearly of a globular or oval form, of a white colour, and about 2 lines in diameter. Of 25 specimens of H. pusiola, eight bore these parasites under the abdomen ; some specimens had two, and upon one I found no less than three of them. I propose to describe these more fully on some other opportunity."

^{*} This is also noticed by Lovén in his annual Reports.

^{† &}quot;I should perhaps not have ventured to mention this creature decidedly as a distinct animal, if I had not seen the eggs rush out on opening a specimen; these, when examined under the microscope, exhibited fully developed young, consisting of an anterior body and an abdomen or tail, the atter provided with swimming feet or bristles," &c.—Kröyer.

I am not aware that Professor Kröver has since published anything upon this subject; but from the preceding it is evident, that at least the two first-mentioned vermiform species are true Peltogastri, and that the third must also be placed very near this genus, notwithstanding the difference in the form of the body, appears from the fact that Kröyer places them all in one and the same genus. If the interesting observation upon the young given by Kröyer in the preceding note applies to all the three species, it becomes a positive observation of the Crustacean nature of the vermiform Peltogastri; but if it applies only to the third and last form-to which, as is evident from the text, the note in which the observation is given particularly belongs,-it is at any rate a new confirmation of the opinion that these sac-like structures, filled with eggs, which occur under the abdomen of the long-tailed crabs, are themselves to be regarded as Crustacea.

Even if it may remain doubtful to which of the smaller natural divisions of the Crustacea the genera in question are to be referred, the above-mentioned observations upon the form of the young show distinctly that they are Crustaceous animals; so that it is evident they cannot be represented in our systems as hermaphroditic animal forms. As long as it is not universally admitted that the separation of the sexes, or unisexuality, is a general rule (not to say, law) in nature, and that in our science it must not be admitted that any single animal possesses an opposite sexuality or hermaphroditism, without a scientific proof of this abnormal behaviour with regard to this particular animal, the opponent of hermaphroditism, which is still ascribed to a good many animals, must find himself in this position,that the sexual relations of the less known and uninvestigated animal forms are adopted from the relations of those animals which are most nearly allied to them, and which have been submitted to a closer examination in this respect, although innumerable examples of the uncertainty of this procedure are sufficiently well known. Thus, as long as the two genera of parasites under consideration could be regarded as Hirudinoid animals, we were under the necessity of supposing them to be hermaphrodites, although this point was not only not proved, but had never even been investigated, but because all the Hirudineæ were regarded as hermaphrodites. But if we now know that these animals are Crustacea, and agree that all the Crustacea-with the exception of most of the forms belonging to the group of Cirripedia, to which they can scarcely be referred-are to be regarded as animals with separate sexes, these parasites must also be considered from analogy as unisexual animals. To show this, and to prove that it was far from right to seek in these

fixed parasitic forms for representations of hermaphroditism, was the principal object of the preceding remarks, in which I have endcavoured to give a better view of our knowledge of these parasites.

As, however, we have been directing our attention to these shapeless and somewhat enigmatical Crustacea, I will not omit, in conclusion, touching upon the question as to the positive systematic position which they may possibly occupy, in order to remind the reader of one or two remarkable circumstances, which perhaps may not be without their value in the solution of this problem.

Thus, it is known that in his Peltogaster Paguri, Rathke found some (eight) small Crustacea, scarcely one line in length; they were in the large cavity which occupied the greater part of the body of the animal, and contained an extraordinary quantity of developed eggs, so that this observer regarded the cavity as a combined digestive and hatching organ. That this cavity, to which the opening at the free end of the body forms an entrance, certainly serves for the latter purpose, we know with certainty from Cavolini's observations; and these small Crustacea were, therefore, contained in an ovisac (Bruthöhle) together with ova in course of development. In the work above quoted, Rathke has described and figured these Crustacea under the new systematic name of Liriope pygmæa; but, remarkably enough, has regarded this new genus as a form of the Amphipoda,-I know not for what reason, for the characters given do not appear to me to indicate that relation, nor do the figures remind one of an Amphipode. We are rather struck with the great resemblance of the young of the Isopodous genus Bopyrus to these small Liriopæ, and at least one cannot doubt for a moment that the form in question is Isopodous. They appear to differ in no essential points from the larvæ of the Bopyri which are known to us, especially from the observations of Kröyer and Rathke; they are only more elongated than the previously described larvæ of the Bopyridæ. Now, as it is well known that the Bopyri are parasitic under the carapace or abdomen of other Crustacea, we might suppose the relation between the Liriopæ and the Peltogaster in which they were found, to be of this nature : that the former, instead of serving, as supposed by Rathke, for the nourishment of the Peltogaster, led a parasitic life like other Bopyridæ, in the ovisac of the latter, which, as we are now aware, is a Crustaceous animal. There are, however, other circumstances which sufficiently prove that the relation may be quite of another nature.

In the above-mentioned memoir of Cavolini, which is so rich

in excellent observations, we find a representation of a very remarkable irregular mass (fig. 19), which was quite full of more or less developed ova. It was found in a crab, attached by one end to the inner wall of the stomach, and with the opposite extremity somewhat squeezed in between two of the partitions, which indicate the limits of the lateral parts of the original rings of which the carapace is composed. In fig. 18 m n, Cavolini has represented the ova contained in this mass in various degrees of development, and in fig. 18 r r, two embryos just after their exclusion from the egg. Cavolini compares these embryos with the Onisci squilliformes described by Pallas, and confers upon them this name. We cannot help seeing that the embryos thus described and figured, are so very closely allied to Rathke's Liriope, that they could not be distinguished without difficulty, and we are consequently led involuntarily to compare them with the larvæ of Bopyrus. The form of the young larvæ, therefore, shows, that this irregular, ovigerous mass is in all probability not only a transmuted parasitic Crustacean, but that it also belongs to the family of the Bopyridæ, only it is more shapeless, or, as we might say, more monstrous than any other developed form of that family, more even than the Peltogastri and Pachybdella, and consequently this parasite is something more than an Epizoon; for it was attached to an internal organ, like an Entozoon, or intestinal worm, and especially like the extraordinary mollusk Entoconcha mirabilis, discovered by J. Müller in Synapta digitata*.

We have now got the following facts together :-- The Bopyridæ are known only as parasites upon the higher Crustacea,--the less irregular species of the genus Bopyrus occurring under the carapace of the long-tailed Crustacea (Macrura), and the most irregular, with which Rathke has even formed a separate genus, under the abdomen of the same animals. The latter forms consequently agree essentially, both in their residence and external conditions of life, with Peltogaster and Pachybdella, which, as we have seen, live under the abdomen of Paguri and Crabs (Brachyura). Moreover, they approach these two parasites to a certain extent even in their form. Thus they differ from the more regular species of the genus in having the limbs, with the exception of the anterior pair, completely lost on one side of the animal; and the cavity for the reception of the eggs, which occurs so universally amongst the Isopoda, instead of being formed of several equally developed plates, is here composed principally of a single plate, which has been developed at the

* See Annals, 2nd Series, vol. ix. pp. 22 and 103, Jan. and Feb. 1852.

expense of the others, and forms by itself a spacious pouch with a large opening. From this we might say, that they form a sort of transition to Peltogaster and Pachybdella, whose ovisacs might perhaps be represented as resulting from a further development of the single large lamina of Bopyrus, and whose feet must then be considered as having disappeared at once from both sides of the body. To this may be added Rathke's observations, who found the Liriopæ, resembling the larvæ of Bopyrus, amongst the eggs in the ovisac of Peltogaster Paguri, and Cavolini's observation of the development of Liriope-like larvæ from the eggs contained in an irregular sac, which cannot properly be placed far from Pachybdella and Peltogaster; and the question then forces itself upon us, whether we must not suppose that there is an actual and close relationship between these two parasites and the Bopyridæ, and especially whether we must not admit the existence of a more intimate connexion between Peltogaster Paguri and its Liriope, than that the latter is parasitic in its ovisac.

Supposing Peltogaster and Pachybdella to be Bopyridæ, the Liriopæ might either be regarded as the more advanced larvæ of the Peltogaster in which they were found, or as the young state of the male parasite, for it is well known that the males of the Bopyridæ are very different from the females and live as parasites upon them. None of these suppositions can however be proved at this moment, unless we are in a position to recognize a remarkable resemblance between the larvæ of the Bopyridæ and the Crustacean embryos, which Cavolini and Kröyer have found in our parasites. Neither the short notices given by both these authors, nor the figures published by the first, are sufficiently perfect for this purpose; but on the other hand, they do not appear to stand in the way of such an opinion. The feet with swimming bristles, mentioned by both and represented in Cavolini's figures, may very well represent the abdominal feet of a Bopyrus; and even the circumstance that no mention is made of the thoracic feet which are so characteristic of the Bopyridæ, cannot be taken positively as a proof that they were not present, as they might have been so pressed under the belly, that they would only become visible on more careful examination. It even appears from Cavolini's statements about the projecting branchial laminæ, seen when the animal was observed from beneath, that he must have seen something, which might be regarded either as these feet, or perhaps as the branchial laminæ of the Bopyridæ; nay, we cannot exactly understand how Cavolini can have compared his young animals with O. F. Müller's figure of Cancer paludosus, unless they had possessed such feet, or presented quite

different forms from the one in which he has figured them. From the similarity to the *Cancer paludosus* we might almost be induced to suppose, that his figure represents the animal contracted into the bowed form in which it lies in the egg, and which it may probably have retained for some moments after exclusion,—and the resemblance to the larva of a Cirripede or of some other Entomostracan, might have been produced in this manner.

All this however lies, as I have already said, beyond the object which I had proposed to myself in the present communication, and only furnishes indications which I recommend especially to the notice of those naturalists, who for the study of the lower animals have lately so often visited the coast of the Mediterranean, where these remarkable parasites must, according to the preceding observations, be not uncommon*.

POSTSCRIPT.

Some time since I was informed, by a letter from Dr. Creplin of Greifswald, that Professor O. Schmidt had given a figure and short description of the larva of a Pachybdella in a periodical called 'Das Weltall' for 1854 (No. 3. p. 19), but I have only just (December 1854) been able to obtain this journal. From the figure given by Schmidt, which agrees closely with Cavolini's fig. 16 c. referred to by me, it certainly appears that the young animal is extremely like the larva of an Entomostracan; and this renders still more remarkable the relation above referred to between the Liriopæ of the Peltogastri, which resemble the larvæ of Bopyrus, and the Liriope-like young of Cavolini's extraordinary parasite (figs. 17 & 18 r r). Moreover Schmidt's observations prove that Pachybdella is not only common but even abundant at Wangerooge, and it also appears that Schmidt has collected single specimens of Pachybdella = Peltogaster on the Dalmatian coast.

⁺ The *Peltogastri* which I have been able to examine, for three of which I am indebted to the Zootomical Museum of this University, and for a fourth to Professor J. Müller of Berlin, have unfortunately furnished me with no explanation of the structure of the embryos, as none of them presented eggs with developed larvæ. This was also the case with the specimens of *Pachybdella*.